

Tree Roots and the Use of Soil Nutrients

G. D. BOWEN

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I. INTRODUCTION

This chapter addresses root growth and the ways roots use soil nutrients. Interactions between soil moisture and ion uptake and some aspects of water movement to roots are also discussed. The influence of root growth and distribution on prevention of windthrow will not be examined and morphogenesis of roots and cell physiology will be treated only where they are immediately relevant to the functioning of roots in soil.

The tree root consists basically of a lateral root system in the surface layers of soil and deep "sinker" roots. The large surface laterals produce many smaller branches which in turn produce an extensive system of fine roots, important in nutrient and water uptake and the sites of mycorrhiza formation. The sinker roots (and associated fine roots) are particularly important in water uptake at depth and tree survival in dry seasons, although sometimes they have important nutrient uptake roles as well. Most of the emphasis in this chapter will be on the fine root system.

Early research on tree roots focussed on qualitative or semi-quantitative descriptions of root systems. The emphasis is now increasingly on quantitative aspects, particularly in relation to nutrient and water uptake and plant growth and survival. Quantitative concepts of ion uptake from soil have been developed largely on crop plants over the last 15 years (see Nye and Tinker, 1977). The translation from annual crops to perennial trees, however, involves a number of different considerations which are both dynamic and complex. For example, the perennial plant has a preformed framework on which to grow new roots each year, a framework which stores carbohydrate and nutrients but also costs energy to maintain. The perennial system also involves consideration of root function while the tops of plants are dormant, and the stimulus for regrowth of roots. Furthermore, the plantation tree changes its root environment physically, chemically and microbiologically, during its life-time because of the development of litter layers and because of the redistribution of some elements in the profile.

Perennials and annuals are usually infected by symbiotic fungi to form mycorrhizas which increase nutrient uptake; this phenomenon is also discussed.

II. ION UPTAKE FROM SOIL

There are three major components of ion uptake from soil: the ability of the soil to provide nutrients, their ability to move to the roots and the ability of roots to absorb nutrients which have arrived at their surface.

A. Solubilization of Nutrients

The provision of nutrients by soil systems is discussed in Chapters 4 and 5. However, the root may also affect the concentration of nutrients in soil solution by release of root exudates and indirectly by reducing moisture in

soil, which subsequently affects mineralization processes and transfer of ions through soils.

The solubilization and chelation of minerals in soil by root exudates or by microbial growth in the rhizosphere are discussed by Nye and Tinker (1977) who considered there is no direct unambiguous evidence for solubilization. However, losses from the roots of cereals of up to 20% of dry weight of the plant have been reported (Barber and Martin, 1976) as root exudates and lysates from aging cells and these could well lead to significant solubilization (e.g. Moghimi *et al.*, 1978). Gardner *et al.* (1982) demonstrated that sterile roots of *Lupinus albus* can break down colloids of Fe/Si, Fe/P and Al/P. Furthermore, some rhizosphere bacteria produce iron chelating "siderophores" which may affect Fe availability to plants (Powell *et al.*, 1980; Kloepper *et al.*, 1980). In tree species, Mulette *et al.* (1974) reported a marked growth response of *Eucalyptus gummiifera* to insoluble phosphates and suggested this may be associated with microbial action. Increases of concentrations of sugars in root exudates of sour orange and of *Eucalyptus pilularis* under nutrient deficiency (Cartwright, 1967; Ratnayake *et al.*, 1978) could also increase solubilization by micro-organisms but this matter needs quantitative evaluation. Root exudation by trees was reviewed by Smith (1976); little is known of intraspecific variation in root exudation and its possible manipulation.

B. Transfer of Nutrients to Roots

Nutrients arrive at the root surface by a mixture of convection (mass flow with the water) and of diffusion along a concentration gradient caused by uptake of ions at the root surface (see Nye and Tinker, 1977). The dominant mechanism for movement of $\text{NO}_3\text{-N}$, $\text{SO}_4\text{-S}$, Ca, Mg and Na under good soil moisture conditions is convection. For K, Mo and B, both diffusion and mass flow are important. Diffusion plays the major role with $\text{H}_2\text{PO}_4\text{-P}$, $\text{NH}_4\text{-N}$, Cu, Fe, Mn and Zn, and indeed some of these, e.g. Cu, are almost immobile in many soils.

The diffusion rate of ions in soil varies with the ion and is very much slower than in water alone, due to the tortuous pathway through soil pores and to interactions with clays and organic material. For both convection and diffusion, the tortuosity factor increases considerably as the soil dries, and larger pores are no longer filled with water; for example at -0.1 M Pa suction, water menisci in soil retreat to voids less than $1.5\text{ }\mu\text{m}$ in diameter, which are inaccessible even to root hairs. Over a field moisture range of -0.01 M Pa to -1 M Pa , diffusion through soil can decrease by two orders of

magnitude for some ions (Nye and Tinker, 1977). In a sandy soil, Clarke and Barley (1968) found the diffusion coefficient for $\text{NO}_3\text{-N}$ at 0.05 volumetric water content to be one-fifth that at 0.20.

In a clay, the supply of a poorly mobile ion such as H_2PO_4^- would be restricted to soil between the root hairs (when they occur) and only a small distance beyond (less than 1 mm), but in a sandy soil with less adsorption of H_2PO_4^- , diffusion would occur for a wider radius, perhaps 2–3 mm in a week (Heinrich, 1982). As soil dries, more highly diffusible ions (such as K^+) move to the root over much smaller distances and thus the soil is used less effectively. Below a certain soil moisture there could be a sharp cut off of transfer to the root because roots may shrink, reducing contact with the soil, but this has received little study.

C. Absorption Ability of Roots

The absorption ability of roots is their ability to absorb ions independent of soil transfer factors, i.e. uptake from a stirred solution. Uptake can be passive (along an electrochemical potential gradient) or can be active (i.e. against such a gradient). Most anions and most of the essential cations enter cells actively, as indicated by biophysical studies and by the elimination of uptake by metabolic inhibitors such as cyanide and anaerobic conditions. Allelopathic compounds such as phenols may well affect root function and ion uptake by such an inhibition. Uptake of ions is selective; they enter at different rates and some are normally excluded, e.g. Na. However, with extreme nutrient deficiency and soil toxicities such as high salinity, the plasmalemma can lose control of this selectivity (also releasing cell contents) to the plant's detriment.

Absorption is usually high near the apex of the young, unsubsized root and by mycorrhizas, (Bowen, 1973). The absorption ability of a root is magnified greatly by the production of numerous laterals along them, each with a metabolically active apex. In tree roots short laterals soon cease apical growth, become subsized and their absorption ability declines, whereas the absorption ability of those which have become ectomycorrhizas can remain high for several months (Bowen, 1973). However, high absorption ability is certainly not always restricted to the apex and to mycorrhizas. Bowen (1970) showed that roots of *Pinus radiata* (radiata pine) seedlings grown at soil temperatures of 16°C (and lower) have a sustained uptake for H_2PO_4^- along the root and this probably corresponds with sites of accumulation of translocated assimilates under these conditions (Rovira and Bowen, 1973).

Chung and Kramer (1975) and Sands *et al.* (1982) found that the

permeability to water of suberized parts roots of *Pinus taeda* (loblolly pine) was 40–70% of that of unsuberized roots. The former also showed that suberized parts of roots could have 60% of the H_2PO_4^- absorption ability of the unsuberized root. Considering the extremely large amount of suberized root on trees, it has been argued that suberized roots may be the major route of nutrient uptake. However, the studies above were in solution and it is possible that the intimate root–soil contact, effected by plant mucigel in young roots (Foster, 1982) may be small with older roots. This important consideration appears not to have been studied because of technical difficulties, and there is a pressing need to develop reliable methods of examining ion and water influx to different parts of root in a *soil* environment; the elucidation of this point is critical to our appreciation of nutrient and water uptake from soil.

D. The Uptake System

The uptake of nutrients by the tree is determined by nutrient transfer in soil to the root, root abundance (see Section III) and the absorption ability of the root. Data on absorption ability in tree species is sparse, but calculations on data of Bowen (1969, 1970) on *P. radiata* show influxes of H_2PO_4^- to be similar to those for agricultural plants for the unsuberized parts of roots. It is reasonable therefore to conclude that as for agricultural plants, in all but highly fertile soils, the limiting factor in uptake of ions moving to the root by diffusion is not usually the absorption ability of the root but the *movement* of ions to the root. That is, uptake from each soil horizon will be governed largely by rooting intensity in that horizon and the extent to which mycorrhizal fungi supplement this (see Section IV, B). This is seen from Fig. 1 (from Barley 1970); low rooting intensities can deplete the soil supply of nitrate relatively quickly, but for poorly mobile ions soil depletion is approximately proportional to the amount of root.

The curves of Fig. 1 relate to a soil at field capacity, but as the soil dries and ion mobility decreases (see above), the curves are displaced downwards so that for even highly mobile ions root length becomes increasingly important. With ions which do not interact with soil colloids e.g. NO_3^- , drying is accompanied by increased concentration of the ion. Over a period of water stress a marked decrease in nutrient uptake can occur (Bowen and Cartwright, 1977). This is due to a decreased transfer of ions to the root, a possible reduction in root absorption ability associated with reduced plant assimilation (caused by moisture stress) and to morphological factors such as more rapid suberization of roots with water stress (see Bowen and Cart-

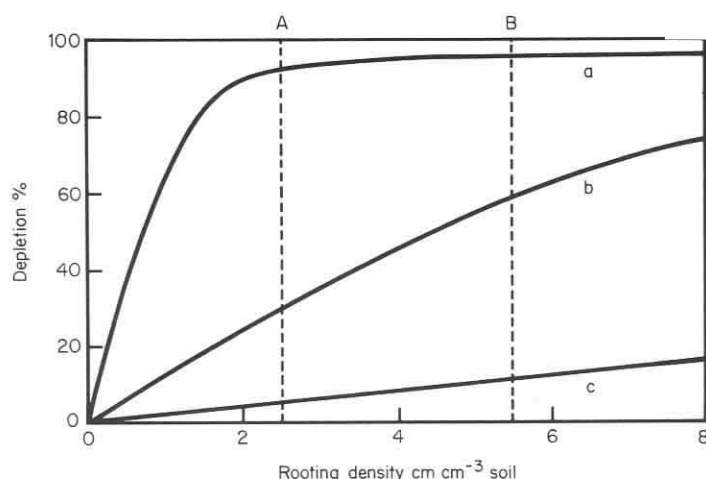


Fig. 1. The influence of rooting density, L_v , on the depletion of labile pools of nutrients. Curves a, b, and c represent the depletion curves for highly mobile ions (e.g. NO_3^- , SO_4^{2-}) poorly mobile ions (e.g. K^+ , NH_4^+ , H_2PO_4^-) and immobile ions (e.g. Cu^{2+}) in a soil at field capacity. A and B are referred to in the text. (from Barley, 1970).

wright, 1977; Leshem, 1970). Uptake of macronutrients essentially ceases in dry soils, but Cu and Zn uptake by ryegrass has been reported in dry soil (Nambiar, 1977).

The relationships of Fig. 1 are of basic importance in understanding the use of soil resources by plants. It is in such terms that one must interpret the effects of many soil factors affecting root growth, e.g. root diseases. For example, if root growth decreases from B to A, this may have limited consequences for absorption of $\text{NO}_3\text{-N}$ but be very detrimental to P uptake. I shall return to this again in discussion of mycorrhizas (Section IV, C).

The transfer of nutrients has usually been studied in inorganic soil systems. I know of no studies of diffusion coefficients and transfer factors through organic and litter layers in plantations (where considerable rooting of tree species occurs). The high number of exchange sites on organic matter, plus the probable greater physical discontinuity of pores and voids in litter than in soil, suggest that transfer of nutrients may be much slower in organic layers than in mineral layers of soils, and that physical exploration of litter by roots and mycorrhizal hyphae would be even more important than in mineral soil horizons. However, if concentrations of nutrients in solution in the litter layer are higher than in soil, this may balance the suggested low transfer rates. These matters need further study.

Water uptake. A detailed examination of water uptake is beyond the scope of this book and readers are referred to Whitehead and Jarvis (1981). Water uptake by roots has been described in mathematical-physical terms of *radial* resistance (i.e. movement into the root, through the cortex to the stele) and *axial* resistance (movement up the xylem, which is governed by the number and size of tracheids or vessels). In the soil-plant system, the dominating resistance, especially in moist surface layers of soil, is the root radial resistance. However, in coarse sandy soil (even near field capacity) and in other soils below -1 MPa potential (approximately), transfer of water through soil is limiting and root length largely dominates uptake. Passioura (1981) raised the possibility that at soil water potentials less than -0.1 MPa, the major resistance to water flow may be the interface of soil and root (Fig. 2), an area at present poorly understood. Such a resistance could arise if the root-mucigel-soil contact is broken.

Under moderate transpirational demands, a profuse root system will deplete soil moisture more rapidly than will less intensive root systems, which thus tend to be water conservative. A conservative use of water by the less intense root systems of trees will be an advantage however only if they are free of competition from other plants. Serious growth loss by 6 month-old *Pinus radiata* occurred through water stress caused by competing weeds in studies by Nambiar and Zed (1980), but at 30 months there was no such stress in similar plantings (Sands and Nambiar, unpublished). The root

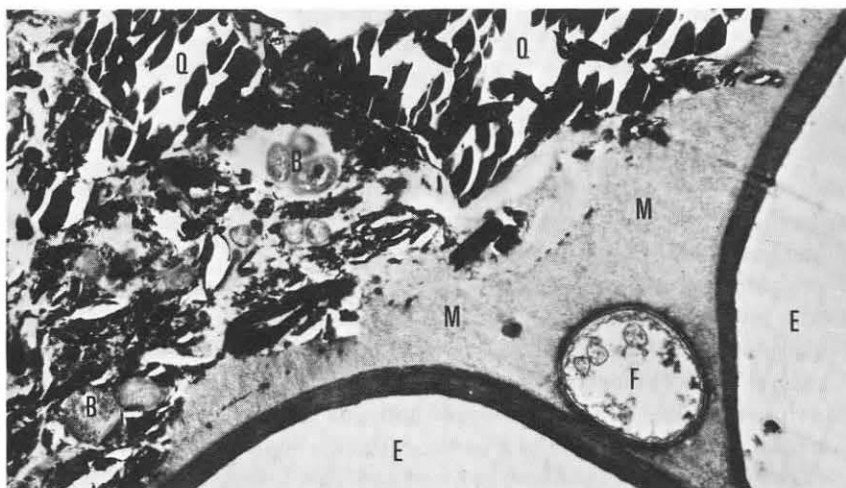


Fig. 2. The root-soil interface. E = root epidermis, M = mucigel produced by root and which penetrates soil, F = fungus, B = bacterial colonies, Q = quartz grains (from Foster *et al.*, 1983). ($\times 7400$)

system had developed well below 100 cm and was able to obtain water at depths not used by weeds (Nambiar, 1981). Slow water use (by low root intensities) may have a further advantage if this leads to slow development of leaf water deficits, for some plants develop an ability to survive short drought only if stress occurs slowly (Spurway, 1980).

III. THE ROOT SYSTEM

The perennial root system of trees contrasts markedly with that of annuals in that the tree has a framework on which fine absorbing roots are produced rapidly throughout the soil when suitable conditions occur. As this is often in advance of shoot growth, carbohydrates stored in the larger perennial roots are used for growth of these roots as well as for maintaining the existing roots. The "permanent" root system also acts as an appreciable store of nutrients, some of which may have been absorbed during the previous growing season, some of which may have occurred by translocation from above-ground parts (especially in deciduous trees), and some of which may have been absorbed by roots during the dormant season for top growth (usually winter). In some eucalypt ecosystems, 40–60% of the macro-nutrients occur in below-ground parts (Bowen, 1980a). Tromp (1983) found that roots of fruit trees were a large store of N (in protein and amino acids) during winter dormancy and that N withdrawn from these during leafing out was of decisive importance to shoot growth vigour (see also Chapter 7).

A. Root Abundance, Distribution and Use of Soil Resources

Fine roots, i.e. usually those below 1–2 mm diameter are, together with mycorrhizas, the main agents in ion uptake and they constitute the major component of root length (see Lyr and Hoffman, 1967). For example, in 39-year *Pinus sylvestris* (Scots pine) (Roberts, 1976), fine roots were 5% of root weight but had 90% of root length. Similarly in 8-year *P. radiata*, they contributed 60–70% of total root length (Squire *et al.*, 1971).

Table I shows many tree species have very low rooting densities (i.e. L_v , cm root cm^{-3} soil) even in the surface horizons, and these are often an order of magnitude less than that of grasses. Although some roots can be found at great depth, e.g. 16 m for *Eucalyptus marginata* (Carbon *et al.*, 1980), generally the greatest proportion of the roots are in the surface layers e.g. in *P. radiata*, 14–26-years-old, only 25–47% of all roots less than 0.4 mm diameter may be below 25 cm (Bowen, 1964). The low concentration of roots below some

Table 1. Root abundance of tree species and of grasses.

Species	Age (yr)	Soil depth (cm)	Root abundance, L_v , (cm cm ⁻³)	Source
<i>Pinus radiata</i>	3-4	0-10	0.13-0.18	Nambiar (1983)
		10-20	0.28-0.34	Nambiar (1983)
		40-50	0.03	Nambiar (1983)
	8	0-10	1.1-2.9	Squire <i>et al.</i> (1973)
	14-26	0-8	2.0	Bowen (1964)
		25-45	0.8	
<i>Pinus silvestris</i>	39	91-106	0.4	
		0-15	5.26	Roberts (1976)
		15-30	1.25	
		45-61	0.34	
		91-106	0.08	
<i>Picea sitchensis</i>	11	surface horizons	1.7-2.8	Ford and Deans (1977)
<i>Eucalyptus marginata</i>		0-10	<8	Carbon <i>et al.</i> (1980)
		50-60	0.2	
		1600	0.005	
Grasses		0-15	50	Barley (1970)
Cereals		0-15	5-25	Barley (1970)
		25-50	4	

50 cm may sometimes obtain nutrients from depth (e.g. with buried soils), but quantitatively this is likely to be small (see Fig. 1) and their main function appears to be water uptake, especially in times of stress. Water behaves as a highly mobile nutrient, and only low rooting-concentrations are needed to withdraw available water: in a podzolized sand with 34-year *P. radiata*, and in a laterite podzol soil with 14–26-year *P. radiata*, in South Australia appreciable withdrawal of water to 2–3 m occurred in summer drought (Holmes and Colville, 1970; Holmes, unpublished). In the latter case, the ratio of actual to potential evaporation was 0.25–0.5. Soil factors inhibiting root growth in lower horizons, e.g. compact soil layers, could place survival of the tree in jeopardy in times of water stress.

Beyond the first two years, apart from higher rooting concentrations around trunks associated with water from stem flow (Reynolds, 1970), radial variation in L_v is small and is mainly related to topographical differences such as mounding (e.g. Ford and Deans, 1977; Nambiar, 1983).

Bayliss (1975) referred to two extreme morphological root types: “graminoid” and “magnolioid”. Graminoid roots are fine (often less than 0.1 mm diameter), profusely branched, and frequently have numerous, long root-hairs. At the other extreme, magnolioid roots (regarded as a primitive root type) are coarse (rarely less than 0.5 mm diameter), have fewer branches, and few and short root-hairs (if any). This category includes *Magnolia*, *Liriodendron tulipifera*, many podocarps, citrus and a number of other tree species (all of which respond well to mycorrhizal infection). That is, “magnolioid” plants usually have low L_v values. Although a great many of the gymnosperms of plantation importance tend to this type, some trees, e.g. some *Eucalyptus*, can have predominantly very fine roots (Barrow, 1977; Heinrich, 1982).

The sparsity of tree roots can be appreciated further by examining their spatial distribution, e.g. Table II (Bowen, 1973) for *Pinus radiata*. With intensively rooting plants, the soil zones contributing nutrients to adjacent roots frequently overlap, and most of the soil volume is used effectively. However, especially for poorly diffusible ions such as $H_2PO_4^-$ and with root distributions such as those in Table II, there are large inter-root volumes of soil which would contribute little to nutrient uptake even under ideal conditions for diffusion, e.g. sandy, moist soil. However, as we shall see, continued root death and growth of new roots into soil, and uptake by mycorrhizas can often compensate for this apparently poor use of soil.

Competition. In plantations trees are growing in communities, often with other plants (especially grasses and other weeds) before canopy closure. Both for poorly mobile and for highly mobile nutrients (including water), the sharing

Table II. Root distribution of *Pinus radiata*.^a

Soil	Long roots		Short lateral roots			
	Closest root ^c		Closest short root			
	Mean distance apart ^b (mm)	range (mm)	mean (mm)	range (mm)	mean (mm)	length (mm)
Lateritic podzol ^d	12.8	2–25	7.6	1–52	9.0	4.4
Sandy solodized ^e	14.2	2–31	9.0	1–44	5.9	4.5

^afrom Bowen, 1973.^bMeans of at least 220 roots. Based on number of long roots in 15 × 15 × 12 cm samples.^cDistance to the nearest neighboring long root.^d0–12 cm under 27-year-old *P. radiata* stand.^e0–12 cm under 20-year-old *P. radiata* stand.

of soil resources is closely related to the relative abundance of active roots. The greater rooting intensity of grasses and other weeds is doubtless an important factor in poor survival and poor response to fertilizers by young trees where weed control is not practised (e.g. Nambiar and Zed, 1980).

Relative rooting ability could be an important factor in the dominance of some individual trees in a plantation but this has not been examined.

B. Fine Root Turnover

The death and replacement of fine roots could affect the extent to which large inter-root volumes of soil are used. Many recent studies suggest that the death and replacement of fine roots is common. Thus Fig. 3 (from Ford and Deans, 1977) shows almost two-fold differences in total length of roots of *Picea sitchensis* (Sitka spruce) <1 mm diameter during a season. Persson (1979) found in 18 year *Pinus sylvestris* stands that the total fine root production in a season was twice that of fine roots present at any one time. Because of technical problems in recovering dead roots, it is likely, however, that most estimates of fine-root turnover are conservative. If fine-root turnover occurs two to several times in a season (as claimed in some conditions), the total length of fine root in a season will be larger than that suggested by a single sampling (e.g. Tables I, II) and similarly, the use of soil resources will be greater, although still not as large as that by “graminoid” roots.

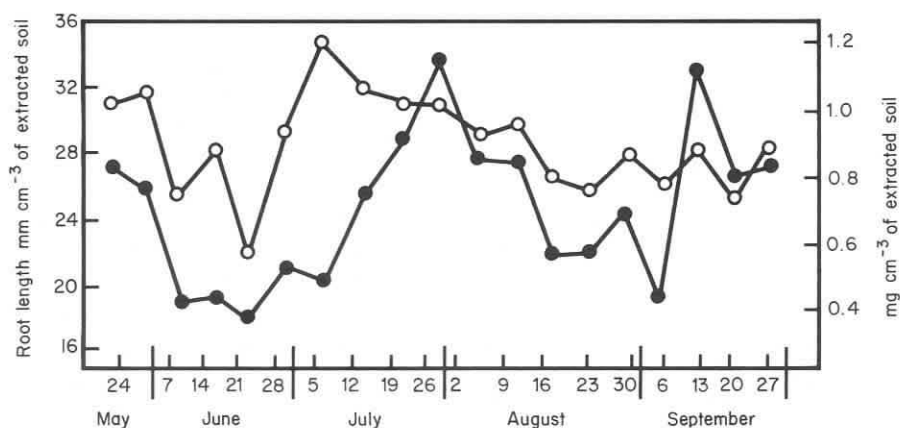


Fig. 3. Changes in the concentrations of fine roots in the eleventh year of a *Picea sitchensis* plantation: ●-lengths, ○-dry weights. (after Ford and Deans, 1977).

Because of the continual loss and initiation of roots, the "cost" of tree roots is considerably greater than that suggested by the 20–30% of the tree biomass which is below ground for both conifers and hardwoods (Hermann, 1977) at any one time. There are now several careful studies indicating that a large part of net primary productivity is directed to the roots and to fine-root growth. Many of the data are for tree-dominated ecosystems, not plantations, and the accuracy of the data on the trees could be affected to some extent by roots of understory plants, but the emerging principle indicated above is the same. Harris *et al.* (1977) considered total root production in a *Pinus taeda* (loblolly pine) plantation ($9 \text{ t ha}^{-1} \text{ yr}^{-1}$) was 2.8 times greater than net annual wood production. In 15–20-year stands of *P. sylvestris* in Sweden, Ågron *et al.* (1980) estimated that more than 50% of assimilated carbon dioxide was used for fine root production, which accounted for 95% of the annual root biomass (Persson, 1980). On a high productivity stand of *Pseudotsuga menziesii* (Douglas fir), fine-root production accounted for 8% of total dry matter production (total root production was 23% of the total biomass of $17.8 \text{ t ha}^{-1} \text{ yr}^{-1}$), and on a low productivity site, fine roots accounted for 36% (total root was 53% of the total biomass of $15.4 \text{ t ha}^{-1} \text{ yr}^{-1}$) (Keyes and Grier, 1981). In 23-year *Abies amabilis* (Pacific silver fir) in the Pacific North-west (USA), 36% of net primary productivity was used for fine-root production (<2 mm diameter), and in a 180 year stand this was 66% (Grier *et al.*, 1981).

Such data do not usually take into account carbon losses by root respiration and the exudation of organics from the root, so the amount of assimilate going to roots will be even larger than the data suggest. One

obvious question is whether the tree needs all of these roots for productivity, and if not, can fine-root production and turnover be managed by selection or by other methods. The answers to such questions must await further *quantitative* evaluation of relations between root growth, use of soil resources, tree demands with time for optimum growth, and genetic variability in root production within and between species.

There is clearly a need for more study of fine-root turnover and factors affecting it. Factors determining fine-root longevity have received little study, but it is clear that soil moisture has a major effect. Deans (1979) found death of fine roots of *Picea sitchensis* occurred with a decrease of soil water tension below -0.02 MPa (-0.2 bar) i.e. at relatively low water stress. Other species may need soil moisture tensions of -0.1 to -0.7 MPa before death occurs (see Section III, C), even though fine-root growth may be slowed considerably before then. Variation between species and soil moisture at different sites may account for reports of fine roots remaining active in some cases for several months and in other cases only for a few days. Nutrition also plays a role: Alexander and Fairley (1983) found fertilizing decreased fine-root mortality in *P. sitchensis* by 30%.

Soil biological factors such as disease and some soil mesofauna can also reduce fine-root biomass. Ausmus *et al.* (1977) considered root-feeding cicada larvae and phytophagous nematodes may consume up to 10% of the standing tree root crop in a hardwood forest. The use of photosynthate for rapid shoot growth can sometimes reduce root elongation (e.g. Ford and Deans, 1977) but does not usually cause their death. Shoot activity and fine-root activity are balanced; for example, severe defoliation of *Abies balsamea* (fir balsam) by spruce budworm is accompanied by a significant increase in death of absorbing roots (Stilwell, 1960). In temperate climates there is a marked loss of fine roots in winter, probably associated with cessation of shoot growth: Keyes and Grier (1981) found that in a 40-year *Pseudotsuga menziesii* stand, the living fine-root biomass was 8.3 t ha^{-1} in June but 2.1 t ha^{-1} in December. With plantations in climates with marked wet and dry seasons, e.g. *Pinus radiata* in southern Australia, there is likely to be a high fine-root mortality in the dry season, but with plantations in uniformly moist soils in warm climates, there may be less marked fluctuations of the fine root population and perhaps a relatively stable "steady state" exists (there could still be considerable death and initiation of roots). Reynolds (1975) considered that taking a reasonable estimate of the respiration of fine roots, they would consume their own dry weight in energy reserves in one week during the growing season. This may be an overcalculation for it would call for a very much greater percentage of assimilate going to the root system than that given in other studies. Never the less, Reynold's suggestion (1975) that death of fine roots is energy conserving in environments in which they

make little contribution to tree growth (e.g. in dry soils) is attractive. The possible large fluctuations in fine root numbers and their significance as an assimilate sink suggest that it is important to take these fluctuations into account in studies of carbon balance of trees and assimilates going to roots (see Chapter 8). Simple extrapolation from above-ground biomass using allometric formulae are certain to be grossly in error. The assimilate costs of mycorrhizas are discussed in Section IV, C.

The recognition of the high turnover of fine roots has had an impact on traditional thinking on nutrient cycling in forests; in some situations fine-root turnover may be a more significant factor in nutrient cycling than is litter fall. Estimates of the fine-root necromass pool vary from 0.25–0.5 of the input from litter fall (in 35-year *Picea sitchensis* in Scotland, Fairley and Alexander, 1983) to at least twice the litter fall (in 15–20 years *Pinus sylvestris* in Sweden, Persson, 1978). Fogel (1980) concluded that in an oak-hickory stand the throughput of fine roots (≤ 5 mm diameter) releases twice as much N as the litterfall and that in a *P. taeda* plantation, N released in the fine root fraction contained 84% of that in litterfall but released twice the N on decomposition. Vogt *et al.* (1982) estimated that fine roots plus mycorrhizas in a stand of *Abies amabilis* cycle some 4 times the N, 6–10 times the P and K, 2–3 times the Ca, and 3–10 times the Mg as does litterfall. Decomposition of fine roots is usually rapid (Fogel and Hunt, 1979). The case for fine-root turnover as a major component of nutrient cycling is strong—another area needing more study.

C. Root Initiation and Growth

It is important to appreciate factors affecting the (separate) criteria of root initiation and root growth, not only in regard to root regeneration following transplanting but also for examining the management of nutrient uptake during and between seasons (e.g. by timing of fertilizer addition). A knowledge of root regeneration is also important in assessing potential recovery from root disease. Many of the factors affecting root growth are discussed in detail by Lyr and Hoffman (1967) and Hermann (1977). Generalizations are of limited specific use, for information must be obtained for each species of interest to the forest scientist.

Soil temperature. Initiation and growth of tree roots can occur from 2°C to 35°C (Lyr and Hoffman, 1967) (with optima usually between 20°C and 30°C), but there is very great variation both between species and within species. Figure

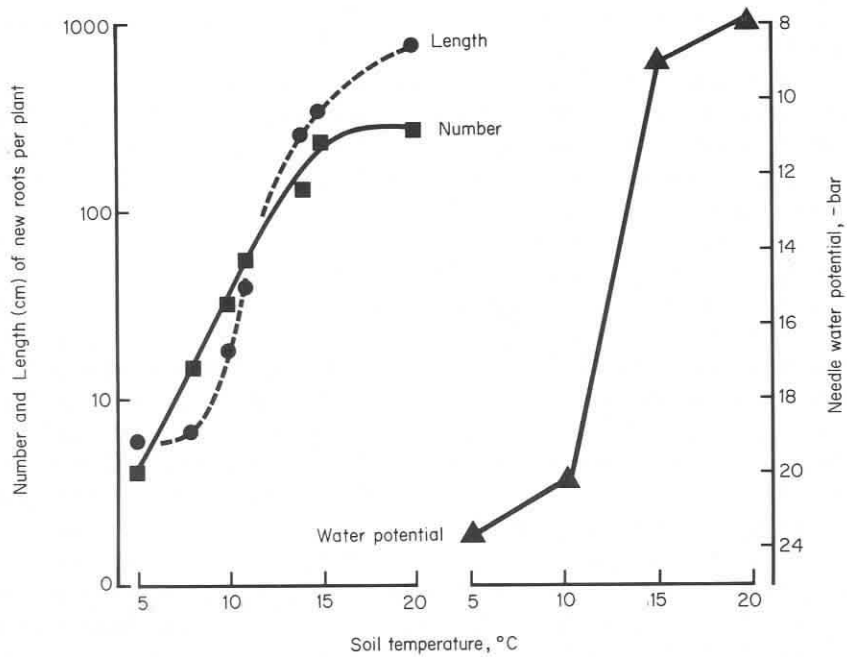


Fig. 4. Effect of soil temperature on new root growth and on mid-day needle potential in 8-month *Pinus radiata* seedlings 32 days after transplanting to a sandy forest soil. Data of Nambiar *et al.* (1979, 1982) (after Nambiar, 1983).

4 indicates that root initiation and growth of transplanted *Pinus radiata* is very slow at soil temperatures below 10°C but rapid at 15°C (and above) and that root regeneration has a large effect on the water potential of the needles. Planting out seedlings of this species in winter when the soil temperature is below 14–15°C is likely to lead to plant water stress.

This is also the period of rapid leaching of fertilizer applied to sandy soils and with poor root-growth, recoveries of applied N fertilizers are low (Nambiar and Bowen, unpublished). The water stress is exacerbated in transplanted seedlings because lifting breaks the intimate contact between root and soil (Sands, 1984). In this species, large soil temperature x genotype interactions occur in root regeneration (Nambiar *et al.*, 1982), and with eight open-pollinated families of *P. radiata*, up to 9-fold differences occurred in new root apices per family at 8°C soil. At 32 days there were up to 3-fold differences in new root length between families at 11°C. Root-regenerating ability was highly heritable and there is a case of selection of

this character for better establishment and for early season growth in some climates.

Root growth generally begins in spring at lower soil temperatures than does shoot growth, and this occurs by mobilization of starch reserves in the existing roots (e.g. Ford and Deans, 1977). Practices such as thinning which can increase soil temperature are likely to lead to earlier root activity in the spring.

Soil water and aeration. Section III, B referred to the possible loss of some fine roots (usually short lateral roots) even at low moisture deficits. With roots showing indeterminate growth, elongation firstly slows and then ceases as soil moisture decreases. Kaufmann (1945) found daily root elongation of *Pinus banksiana* (jack pine) decreased from 3.2 mm to 1.2 mm between 11% and 2% soil moisture. Cessation of growth and metacutinization of root tips of *P. halepensis* occurs at about -0.6 – -0.7 MPa (Leshem, 1970). There are likely to be great species and provenance differences in such behaviour, but in many cases the older literature is hard to interpret because soil moisture percentages are reported rather than the soil water potential.

In many soils, physical factors, e.g. changing soil strength and concentration of salts, can affect root growth rather than moisture *per se*; the physics of root growth has been discussed by Sands (1983). Where no appreciable mechanical impedance occurs roots should be able to grow to -1.5 MPa (Hsiao, 1973), although rates of root elongation start to decrease at about -0.05 MPa, where osmotic forces contribute considerably to water potential (Kramer, 1969). Water stress can also lead to increased solute concentration in roots so that root growth may continue even though leaf growth is checked (Sharp and Davies, 1979). Decreased root elongation and decreased movement of water and nutrients in drying soils can be partly compensated for by increased root-hair growth in some species: in *medicago* the root-hair length trebles between -0.19 MPa and -1.4 MPa (Reid and Bowen, 1978b).

The importance of water distribution to fine-root growth and distribution is indicated by their profusion around tree trunks when stem flow is significant (Reynolds, 1970). Roots also frequently traverse zones of low soil moisture and proliferate once again in areas of high soil moisture (Lyr and Hoffman, 1967).

Excess water can reduce root growth and a high groundwater table tends to lead to a layer of roots at the groundwater interface. Growth in the watertable can be poor because of poor aeration and accumulation of toxins;

the several theories of waterlogging effects on root growth and metabolism are discussed by Cannell and Jackson (1981). Lack of oxygen can be overcome by trees which transport it from shoots to roots e.g. some species of *Salix*, *Alnus* and *Betula* (Lyr and Hoffman, 1967). There is considerable species and provenance variation among plantation species in tolerance of low oxygen e.g. *Pinus contorta* roots are more tolerant than *Picea sitchensis* roots, and this is associated with oxygen transport in the root (Philipson and Coutts, 1978).

Nutrition factors. Increased soil nutrient levels from fertilizer applications often stimulate root growth, particularly in the enriched area (and also secondarily in other areas, due to increased growth of the plant). It is often difficult to distinguish a specific effect of the nutrient on lateral initiation and growth from that due to preferential photosynthate transfer to actively growing roots in the enriched area. Philipson and Coutts (1977), using a split-root technique, found N and P but not K-stimulated rooting of *Picea sitchensis* and that there was also a preferential flow of assimilates to treated roots. Interpretation of such studies would be assisted by examining lateral root frequencies. For example, Nambiar (1980) reported that for *Pinus radiata*, growth of first, second and third order laterals was increasingly affected by N and P deficiency. However, a calculation of the number of laterals cm^{-1} of the next lower order of lateral showed no effect of N-P deficiency on lateral initiation. Nambiar also showed that deficient roots were finer and that root/shoot ratios decreased when deficiencies were corrected; this is consistent with experience on agronomic plants and on other trees, but some pot studies (Barrow, 1977) suggest marked effects on root/shoot ratios may not always occur with tree species.

Root proliferation around pockets of fertilizer is commonly observed in forestry practice. In areas of low rainfall these pockets are rapidly dried by the high root intensity, and this probably leads to cessation of nutrient uptake from them.

Various inorganic ions are noted for their deleterious effects on roots, e.g. excess Al (often associated with low pH), excess Cl or Na, and calcium deficiency (see Hermann, 1977). Large species and provenance differences occur in tree susceptibility to these factors (e.g. salinity, Sands, 1981). In addition, selected mycorrhizal fungi may compensate somewhat for reduction in rooting due to such soil factors (see Section IV, D). Many naturally occurring organic compounds affect root growth and this topic is discussed by Fisher (1979).

Soil physical factors. The effects of soil mechanical strength on root growth are discussed by Sands (1983b). One applied aspect of this is the decreased root penetration often found in compacted soils (see Chapter 14). Considerable species variation exists in growth in compacted soils: Minore *et al.* (1969) showed that *Pseudotsuga menziesii*, *Pinus contorta* and *Alnus rubra* (red alder) could penetrate soils at a soil bulk density of 1.45 g cm^{-3} (but not 1.59 g cm^{-3}), but roots of *Picea sitchensis*, *Tsuga heterophylla* (western hemlock) and *Abies amabilis* could not.

IV. MYCORRHIZAS

Micro-organisms are always associated with roots and are sustained by energy sources from the root (Rovira *et al.*, 1983). Even non-infective rhizosphere micro-organisms affect root growth, root hair growth and nutrient uptake (Bowen and Rovira, 1968) and an extreme example of this is the great stimulation of lateral rooting in some plants (especially Proteaceae) which are known as "proteoid" or "cluster" roots and which greatly increase nutrient uptake (Bowen, 1980a). Infective organisms usually have a greater impact on nutrition than non-infective. However, the major beneficial infecting organisms are N-fixing symbioses of legumes and of non-leguminous trees (see Chapter 13) and mycorrhizas, which increase nutrient uptake. Mycorrhizas of legumes and N-fixing trees such as *Alnus* and *Casuarina* also enhance N fixation considerably by increasing uptake of nutrients such as phosphate. Various types of mycorrhizas occur (see Harley and Smith, 1983), and with the exception of those on orchids, they all function similarly. Here I discuss only the two major types important for forest trees, viz. ectomycorrhizas (ecm.) and vesicular-arbuscular mycorrhizas (v.a.m.).

A. Mycorrhiza Form and Occurrence

Ectomycorrhizas, once thought to be restricted to Pinaceae, Betulaceae, Fagaceae, Myrtaceae and a few other angiosperms, have now been found on many more groups, including a number of legumes, some Casuarinaceae, and several other families (Warcup, 1980). The majority of forest trees presently grown in plantations form ecm.; some of these also have v.a.m.

(e.g. casuarinas, legumes, and eucalypts). Ectomycorrhizal fungi infect the short lateral roots, grow between the cortical cells (usually without infecting them), and produce a "Hartig net" enveloping the cortical cells. Outside the root they form a fungus sheath, or mantle, which may be either inconspicuous or well developed, and variously coloured from cream, orange, pink, salmon to black. Individual hyphae grow from these into soil but often there are conspicuous aggregations of hyphae (mycelial strands) which branch frequently and permeate soil and litter (Fig. 5a). Although the fungi do not penetrate the cortical cells, they can induce a radial extension of them and other physiological effects such as an increase in the nucleolus of the cell. In *Pinus*, ecm. are dichotomously forked (Fig. 5a), sometimes repeatedly to give a coralloid mass, and in other plants, e.g. eucalypts and Douglas fir, this branching can take a pyramidal form or can lead to a "nodule" of mycorrhizal branches bound together by mycelium. Ecm. are formed by a great many basidiomycetes, some ascomycetes and one or two phycomycetes (*Endogone* spp.) (Trappe, 1962, 1977). Some of the ecm. associations are relatively specific, many are not: Molina and Trappe (1982) found in the Pacific north-west of the USA, that *Pinus contorta*, *Pinus ponderosa* (ponderosa pine) and *Pinus monticola* (western white pine) showed few differences in the fungi infecting them but some fungi were able to form ecm. only with *Pseudotsuga menziesii* and *Larix occidentalis* (western larch). Characterization and classification of ecm. is discussed by Zak (1973).

Vesicular-arbuscular mycorrhizas. Most plants can be infected by v.a.m., with the exception of many of the species forming other mycorrhizal types, and a few families such as Brassicaceae, Chenopodiaceae, Cyperaceae and Polygonaceae. The important plantation genera forming v.a.m. include *Casuarina*, *Linodendron*, *Eucalyptus*, *Araucaria*, *Podocarpus* and *Agathis*. The hyphae grow in the rhizosphere and also grow into soil but they do not form a sheath around the root or produce marked changes in root morphology. Therefore, although extremely common, they are harder to recognize than ecm. The fungi occur in most soils and invade the root, growing between the cortical cells, sometimes producing "vesicles" there and entering the cortical cells where they also form vesicles and finely branched "arbuscules" (Fig. 5b). The arbuscules are the major sites for transfers of nutrients to the root and of sugars and other metabolites from the root to the fungus. "Physiological" interactions occur here as with ecm. and are indicated by an increase in the nucleus of the plant root and a 20-fold increase of root cytoplasm in infected cells (Cox and Tinker, 1976). V.a.m. are formed by some 75 fungal species (so far) in four genera (*Acaulospora*, *Gigaspora*, *Glomus* and *Sclerocystis*) in the

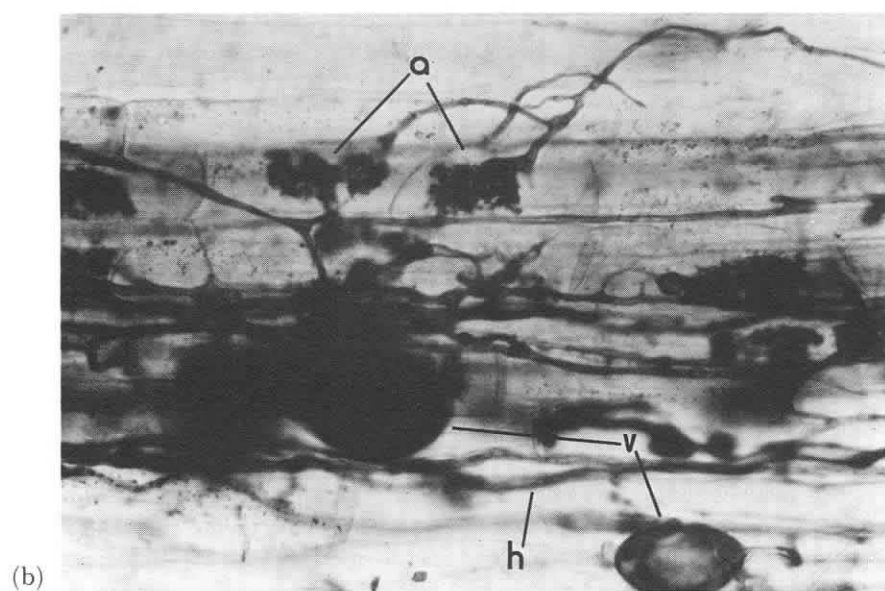
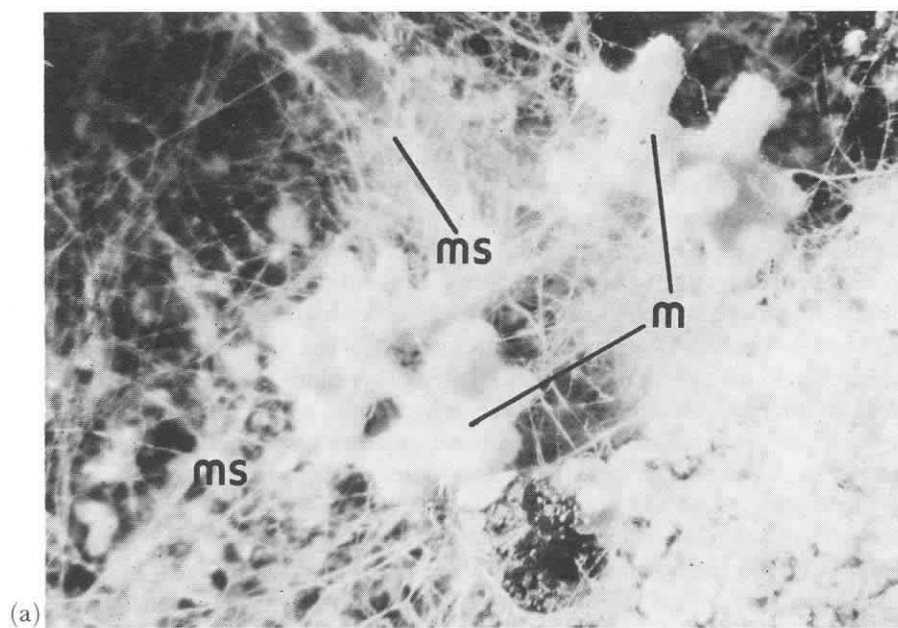


Fig. 5. (a) Ectomycorrhizas of *Pinus radiata* showing dichotomous forking, fungal mantle (m) and mycelial strands penetrating soil (m.s) ($\times 10$); (b) L.S. of Vesicular-arbuscular mycorrhizal infection of a root showing internal hyphae (h), vesicles (v) and arbuscules (a) ($\times 250$).

Endogonaceae (phycomycetes) (Trappe, 1982). The fungi occur in practically all soils, but soil type, climate and management practices determine the dominant species present and its population (e.g. Schenck and Kinlock, 1980; Abbott and Robson, 1982). There appears to be little specificity in infection, most of the fungi having a wide host range, but there can be large differences in their effectiveness in stimulating nutrient uptake.

In summary, most trees used in plantation forestry and plants used in management (e.g. cover crops), are infected with mycorrhizal fungi. There is a large gene pool of mycorrhizal fungi to select from and they give the plant scientist another powerful approach to managing plant productivity.

B. Modes of Mycorrhiza Action in Nutrient Uptake

There are a great many reported responses to inoculation both with ecm. and v.a.m. in glasshouse and nursery studies e.g. for ecm.: in a sand culture of *Pinus elliotii* var. *elliotii* (slash pine), increases in dry weight 28–500% and 5–17 times increases in N, P and K were obtained by Lamb and Richards (1971) and Marx *et al.* (1978) obtained a growth increase of 125% in *Pinus taeda* (loblolly pine) inoculated in fumigated nursery soils; for v.a.m.: Bevege (1971) reported a 10-fold dry weight increase, a 10-fold increase in N uptake and a 20-fold increase in P uptake following inoculation of *Araucaria cunninghamiana* (hoop pine) in a fertile red loam, while Kormanik *et al.* (1977) found 7-fold increases in the height of *Liquidambar styraciflua* (sweet gum) in fumigated nursery plots after inoculation. Field responses are discussed in Section IV, E.

Different fungi stimulate plant growth to different extents and therefore tree productivity can be increased by inoculation with selected fungi. Increases of nutrient content of the plant may be due to increased absorption of the limiting element in that soil or to increased absorption of several other elements following the relief of a deficiency. The only unequivocal resolution of the primary mycorrhiza function is obtained by being able to replace the mycorrhizal stimulation by a particular nutrient (or nutrients). Although much of the research emphasis of mycorrhizas has been on P, they also increase uptake of many other nutrients including K, S, Zn, Sr-90 (a Ca-tracer), Cu and $\text{NH}_4\text{-N}$ (Bowen, 1980b; Bowen and Smith, 1981; Timmer and Leyden, 1980). On general grounds (see below) one would predict increased absorption of many poorly mobile and immobile ions in soil.

There are a few well-founded claims of mycorrhizal effects apart from enhancement of nutrient uptake, i.e. "physiological effects", but most such claims so far are inadmissible in that they compare the physiology (and

ecophysiology) of a large mycorrhizal plant with that of a small, deficient, non-mycorrhizal plant rather than a fertilized non-mycorrhizal plant of the same size and/or nutrient content as the mycorrhizal plant. Similarly, there is no good evidence that mycorrhizas of any type can fix atmospheric nitrogen (Bowen, 1980b). There is good evidence however that v.a.m. hyphae in soil can assist soil aggregate formation significantly, either by means of its own mucilage products or by those of associated bacteria (Tisdall and Oades, 1979). The following discussion focusses particularly on nutrient uptake aspects of mycorrhizas as this is their major consistent effect.

The absorption ability of an ecm. is frequently about that of the most active portion of a rapidly growing uninfected root and can be several times that of short, non-mycorrhizal laterals (Bowen, 1973). However, in contrast to the growing root, the ecm. retains this ability in the one spot in soil for possibly several months, thus increasing the radius over which ions can move to it. Several-fold differences in absorption ability of P can occur between ecm. formed by different fungi, and this is due principally to the extent of mantle development (Bowen, 1973). V.a.m. also have an increased absorption ability, due again to the uptake by the fungus component rather than to an effect of the fungus on uptake by root cells (Bowen *et al.*, 1975). However, these increases in absorption ability are only a small part of the mycorrhizal effect in most soils.

Several experiments have demonstrated that mycorrhizal fungi use the same inorganic sources of P as higher plants do (see Bowen, 1980b) but recent studies suggest certain v.a.m. fungi can use Fe and Al phosphates not available to higher plants (Jehne and Thompson, 1981; Bolan, 1983). Although some ecm. fungi can use $\text{NO}_3\text{-N}$ in laboratory media, $\text{NH}_4\text{-N}$ is the preferred source of N. The ability of certain ecm. to use $\text{NO}_3\text{-N}$ would be valuable in young plantations (especially with cultivation) where nitrification could occur commonly; the high activity of ecm. in $\text{NH}_4\text{-N}$ uptake is particularly appropriate because this is the dominant N form in many forest soils. Few studies have been performed with N nutrition of v.a.m. but $\text{NH}_4\text{-N}$ is probably the preferred form for these also. Mycorrhizal fungi of all the major types can readily absorb a wide range of organic N compounds (and other organic nutrients) (Bowen, 1973; Bowen and Smith, 1981). Stribley and Read (1980) showed ericaceous mycorrhizas can use a range of amino acids as efficiently as $\text{NH}_4\text{-N}$ for growth but uninfected plants could not; this needs study with ecm. and v.a.m. for its implication in "litter feeding" and nutrient cycling is great.

A special feature of both ecm. and v.a.m. is their conversion of P to polyphosphates (Strullu *et al.*, 1981), the form in which it is transported in hyphae. In ecm., these are a form for storage of P in relatively large amounts which is released into the plant as H_2PO_4^- in times of P stress (Harley and

Smith, 1983). The P storage capacity of v.a.m. is relatively low compared with ecm. (Bowen *et al.*, 1975). Polyphosphate granules were found to also contain Ca, K and Mg by Strullu *et al.* (1981), who suggested polyphosphates act as a cation trap in the vacuoles of the fungus. The sheath of ecm. has also been shown to accumulate Cl, Pb and other heavy metals (R.C. Foster, personal communication), and they may protect the root from these toxic elements to some extent.

From considerations outlined in Section II, D, the most important reason for increased uptake of poorly mobile ions by mycorrhizas is the growth of hyphae into soil, absorption of nutrients and their transfer back to the plant. This is especially large in ecm. in which mycelial strands have developed and the ready production of these is an important characteristic of highly effective ecm. fungi for they can permeate the relatively large soil volumes between tree roots (Bowen, 1973). Skinner and Bowen (1974a) demonstrated translocation of P to the root through soil for 12 cm in this way. Fungal development in soil can also be extensive with v.a.m., e.g. some 80 cm of hyphae cm^{-1} infected root has been recorded (Sanders *et al.*, 1977). A large increase in inflow of phosphate in mycorrhizal plants coinciding with mycelial growth has been demonstrated by inflow analysis for both ecm. and v.a.m. (Barrow, 1977; Sanders and Tinker, 1973).

Plant species with low L_v (and poorly developed root hairs) respond to mycorrhizal infection over a greater range of soil fertility than do plants such as grasses (Bayliss, 1975). Indeed, it is thought that some tree species are obligatorily mycorrhizal, only being able to express their full growth potential if they are mycorrhizal, e.g. *Araucaria* (Bevege, 1971).

Fungi vary in their ability to grow into soil, and despite the obvious importance of such fungal growth to the mycorrhizal response, factors affecting it have received little study. Skinner and Bowen (1974b) showed compaction of a podzolized forest sand from 1.2 g cm^{-3} to 1.6 g cm^{-3} reduced mycelial strand growth from ecm. into soil by up to 80%: a factor which would be expected to decrease nutrient uptake substantially. Sands *et al.* (1982) found that ecm. and unsterilized roots had a similar radial resistance to water flow. However, mycelial strands could possibly benefit water uptake in dry/coarse textured soils and in other situations where low unsaturated hydraulic conductivity of soil limits water uptake. Duddridge *et al.* (1980), using tritiated water, showed mycelial strands of *Pinus sylvestris* ecm. can transport water for at least 7 cm to the root. Mycelial strands may also reduce losses by leaching of soil nutrients (see Chapter 3).

C. A Wider View of Mycorrhiza Function

Mycorrhiza function can be explained in terms of Fig. 1 by an increase of "rooting intensity" by mycorrhizal hyphae (Fig. 5a). Except for very low rooting intensities such an increase will have little impact on highly mobile nutrients (e.g. $\text{NO}_3\text{-N}$) but will have a large impact on uptake of poorly mobile nutrients, e.g. for v.a.m. the inflow of P into mycorrhizal plants was some 4–5 times that into non-mycorrhizal plants (Sanders and Tinker, 1973).

However, many factors in soil as well as nutrient deficiency can lead to low rooting intensity; some of these are high acidity, high or low soil temperature, high aluminium, root disease and high salinity. Bowen (1980b) suggested that rather than restricting our thinking only to mycorrhiza function in low nutrient soils, mycorrhizas should be considered as an alternate mode for ion uptake in a range of soil conditions deleterious to root growth. As long as a mycorrhizal fungus is selected which is less susceptible to the deleterious soil factor than the root itself, hyphal growth by the fungus can compensate (at least partly) for the decreased root growth; i.e. in Fig. 1, root growth may be reduced from B to A and the hyphae can restore the "effective root" intensity from A to B and sometimes beyond. The many fungi which can form ecm. and v.a.m. present a large gene pool from which to select for a fungus less susceptible to a particular deleterious condition. This area of mycorrhizal research needs more attention, for it opens a new avenue to improving productivity on a wide range of "difficult" soils: e.g. Marx (1980) reported large mycorrhizal responses on sites such as mining wastes which often have high soil temperatures and other unfavourable soil conditions. Similarly mycorrhizas form a high percentage of fine-root biomass of *Abies amabilis* in winter (Vogt *et al.*, 1980) and these may maintain some nutrient uptake function in that period for later shoot growth.

As the sharing of soil resources between competing species is closely related to their "rooting" intensity, it is highly likely also that mycorrhizas have been of major importance to trees in mixed ecosystems containing grasses and trees (Bowen, 1980b).

Plants also have to compete with soil micro-organisms for nutrients, but the root is spatially disadvantaged in such competition because micro-organisms are at the microsites of nutrient release from organic matter. However, the penetration of litter by mycorrhizal fungi enables the root to compete for inorganic and organic forms of nutrients with micro-organisms at those microsites. Indeed, Gadgil and Gadgil (1975) presented evidence that mycorrhizal fungi may decrease litter decomposition rates by reducing the amounts of nutrients available to the decomposer micro-organisms.

D. The Energy Cost of Mycorrhizas

The energy costs of mycorrhizal systems are discussed by Bowen (1978), Fogel (1980) and Paul and Kucey (1981). Harley (1975) estimated that even omitting respiration, carbohydrate in the sheaths and fruit bodies of ecm. of a temperate forest would be some 500 kg ha^{-1} i.e. 10% of the timber production. This now appears to be a conservative estimate for Vogt *et al.* (1982) calculated the mycorrhizal fungus component of an *Abies amabilis* stand to be some 3000 kg ha^{-1} , i.e. some 15% of primary productivity; 40–50% of the N cycled via fine roots was due to mycorrhizas. Fogel and Hunt (1979) calculated a throughput of ecm. in a young *Pseudotsuga menziesii* ecosystem to be $14600 \text{ kg ha}^{-1} \text{ yr}^{-1}$, i.e. some 50% of the total biomass throughput. They calculated ecm. were responsible for about 43% of the N recycled annually. When the high respiration of ecm. (Bevege *et al.*, 1975) is added to this, the energy costs are indeed large. Under some conditions ecm. are strong sinks for assimilates: Bevege *et al.* (1975) found *Pinus radiata* ecm. to have 15 times the ^{14}C content of adjacent non-mycorrhizal short roots 24 h after exposing the shoots to $^{14}\text{CO}_2$.

One must ask (i) Do the ecm. compete with other plant parts for assimilates? and (ii) Does the ecm. requirement for assimilate reduce plant growth? Unequivocal answers to these need more research. Bowen (1978) suggested that rapid elongation of young, long roots and the development of ecm. occur at different times i.e. a two-phase system occurs, circumventing competition between young elongating roots and mycorrhizas. Regarding the second question there is little doubt that in most moderately fertile soils the assimilate "investment" in ecm. is well worthwhile: 1 cm of root is approximately equivalent in weight to 1000 cm of hyphae. Furthermore, high fertility decreases ecm. incidence (Harley and Smith, 1983) and the potential assimilate drain of ecm. would be diminished considerably where ecm. would be superfluous to the plant's nutritional needs. It is quite possible (see below) that although mycorrhizal assimilate costs are high, the plant can compensate by increased photosynthesis; much depends on the controls of daily photosynthesis.

Similar arguments apply to v.a.m. although to a lesser degree quantitatively, because of the lesser fungal development, e.g. there is no fungus sheath and no large fruit bodies to sustain. Nevertheless, up to 17% of a heavily infected root can be fungal biomass (Hepper, 1977) although it is usually only 1–5% of the root biomass (Bevege *et al.*, 1975). F. E. Sanders, J. K. Martin and G. D. Bowen (unpubl.) found respiration of v.a.m. onion roots to be six times that of corresponding uninfected roots. The data of Paul and Kucey (1981) suggest mycorrhizal plants compensate for high energy

costs by having greater photosynthesis per day. However, in v.a.m. there are a number of cases of high mycorrhizal infection in soils fertile enough for v.a.m. to be superfluous, and of depressions of growth occurring (see Bowen, 1978). Such situations are not likely to occur in plantations under most conditions.

E. The Application of Mycorrhiza Knowledge

The response to inoculation with mycorrhizal fungi in the field depends on the fertility of the site (i.e. responsiveness), the population level of naturally occurring mycorrhizal fungi, their effectiveness relative to other mycorrhizal fungi, and the ability to introduce inoculum successfully and have it persist.

Ectomycorrhizas. Where a tree species is indigenous to a site, it is almost certain that mycorrhizal fungi for it occur also. However, in the absence of another host, the population of ecm. fungi for that species may decline rapidly with distance from the site, e.g. within 2–3 km they may occur only in very low numbers (Bowen, 1963). Where mycorrhizal fungi are absent or low in number, especially in infertile soils and in disturbed soils, inoculation with highly effective mycorrhizal fungi can mean the difference between success and failure in the introduction of a tree species. Spectacular increases in tree growth have occurred following inoculation of introduced pine species into Australia, Puerto Rico and other places (see Marx, 1980).

In many cases trees are planted on sites which already have a background population of ecm. fungi for the species. Often the indigenous fungi are only poorly effective; although responses to inoculation with higher effective fungi may occur, they are not usually as spectacular as in the absence of mycorrhizal fungi. Table III, from Theodorou and Bowen (1970), indicates such a situation in which the experimental site was adjacent to an existing *P. radiata* plantation. Inoculation with the best fungi gave a 33% increase, and there were significant differences between the various inoculated fungi. Differences in growth were established by 6 months after planting out, and a 44% increase occurred after 5 years (the last detailed observation). At similar sites we often obtained lower responses and over six field experiments the mean height response to the best mycorrhizal treatment was 23%, some two years after planting.

Similarly, Marx (1980) reported on a series of sites in which the predominant naturally occurring ecm. fungus was *Thelephora terrestris*; increases in PVI (Plot Volume Index: mean seedling volume \times number of

Table III. Field response of *Pinus radiata* to different mycorrhiza fungi at 36 months.^a

Inoculum	Mean height (cm)	Mycorrhizal infection (%) ^b
<i>Suillus granulatus</i> #5	158.0	81
<i>Rhizopogon luteolus</i> #17D	152.4	78
<i>R. luteolus</i> #10C	146.4	79
<i>S. luteolus</i> #8	134.8	68
Uninoculated	118.5	65
LSD P = 0.05	19.5	4
P = 0.01	24.5	6

^aFrom Theodorou and Bowen (1970). The study site was at Mt Bold, S. Australia adjacent to 10 year *P. radiata*, in loam with quartz and shale.

^bPercentage of short roots becoming mycorrhizal.

surviving seedlings) in plots inoculated with *Pisolithus tinctorius* ranged from 25% on *Pinus taeda* on a North Carolina site to 450% on *P. clausa* (sand pine) on a Florida site. *T. terrestris* is inferior to many other ecm. fungi but is a successful soil colonizer. One of the problems is to select an effective fungus which can displace it, a simple matter where nurseries are fumigated. Strains even within the one fungus species can vary in their effectiveness (Marx, 1981).

No one fungus is likely to be the best under all conditions and there is a need for research to define the optimum soil type-plant fungus combination in forestry practice. For example, in studies on *P. ponderosa* and *P. sylvestris* in the field in North Dakota, *Pisolithus tinctorius* gave little response but the plot biomass of trees 5 years after inoculation with *Rhizopogon roseolus* was 4.6 and 1.8 times that of uninoculated plots of the two pines respectively (Riffle and Tinus, 1982). Soil conditions affecting fungus establishment, high infectivity and persistence of particular fungi are not well understood: soil pH and soil temperature are two important factors (Bowen and Theodorou, 1973). Nutrition can also determine the dominant fungus in a mixture (Alexander and Fairley, 1983), and some fungi can dominate ecm. formation in young trees but be only a minor component of the ecm. flora in older stands. Mycorrhizal selection for optimal stimulation of older trees has received no study; the emphasis has been on vigorous early growth and establishment of the trees.

Inoculation methods for ecm. fungi have been reviewed by Marx *et al.* (1983). Although inoculation can be performed with forest soil or duff, this lacks control, is logistically daunting on a large scale and may also introduce

pathogens. Good commercial inoculation methods have been developed using spores of ecm. fungi (Theodorou, 1971; Marx, 1976) and (more recently) using mass produced mycelium of selected strains of *P. tinctorius* (Marx *et al.*, 1983).

Vesicular-arbuscular mycorrhizas. In contrast to ecm. most soils have some propagules of v.a.m. fungi. Nevertheless, there are now several records of field responses of crops and horticultural trees to inoculation (see Bowen, 1980b) because indigenous fungi are often low in number or are poorly effective on the particular species—soil combination. Kormanik *et al.* (1982) reported that inoculation of sugar maple, red maple, sweetgum, black walnut, green ash, box elder, sycamore and black cherry increased stem weight from 2- to 80-fold in fumigated nursery microplots. The production of high quality seedlings of many such trees (including N-fixing *Casuarina* species for fuel forests) would be enhanced by inoculation with selected mycorrhizal fungi and by nursery management techniques to encourage high populations of v.a.m. fungi. Because v.a.m. fungi cannot be grown in laboratory media, inoculum is produced on roots of various plant species growing in sterilized sand or soil. Infected roots, soil or spores separated from soil can then be used to inoculate seeds or nurseries (Menge and Timmer, 1982). Inoculation of v.a.m. fungi to the large areas involved in direct seeding in agriculture may be difficult, but inoculation is quite feasible for the smaller areas involved in forest nurseries. Inoculum levels in the nursery can be kept high by various management techniques e.g. Kormanik *et al.* (1980) found maize, millet and sorghum as cover crops in a nursery, raised levels of v.a.m. fungi by 7 to 12 times over a season.

V. FUTURE STUDIES

The last decade has seen a large increase in our knowledge of roots and how they function, but compared with knowledge of above ground part of plants, there is still much to be learnt. Many of our ideas on tree root function have been drawn from more detailed studies with annual crop plants. These help in understanding some aspects of root abundance and the uptake of nutrients, but we have yet to fully appreciate these in a context of the tree crop with a life of 10–100 years and in which there are changing seasons and a continually changing environment. We know relatively little about ion uptake from litter layers and transfer processes in them. We know relatively little about root function when the tops of trees are not growing, nor about

the possible role of roots in control of shoot growth by production of growth regulators—a topic which I have not examined in this chapter.

We are now seeing that the roots may account for a major share of the net primary productivity (in some cases well over 50%), largely by the production and turnover of fine absorbing roots. This is far in excess of what static measurements of tree biomass suggest, and is obviously an area requiring much more investigation both to define relationships between root abundance and nutrient uptake, and to enquire if we can “manage” the fine roots. There is a need to study the synchronization of root growth and function, and tree demand for nutrients and water.

Our tools of management of roots appear to be of three types: silvicultural, genetic and microbiological. We have seen indications of genetic differences in a species with regard to nutrition (Chapter 9) and to root parameters such as root regeneration and soil temperature (this chapter), but much remains to be understood on the relevance of such differences to tree growth in the field. To some extent natural selection has given rise to various ecotypes for particular sites, but by understanding, we should be able to improve on this by conscious selection and breeding for particular properties. As we have seen, in mycorrhizas, there is another large genetic pool from which to select and manage nutrient uptake: an alternative root mode which can be employed to assist nutrition in nutrient poor sites and probably in many soil conditions deleterious to root growth.

VI. REFERENCES

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